

MARIANACTIS BYTHIOS, A NEW GENUS AND
SPECIES OF ACTINOSTOLID SEA ANEMONE
(COELENTERATA: ACTINIARIA) FROM THE
MARIANA VENTS

Daphne G. Fautin and Robert R. Hessler

Abstract.—We describe a new genus and species of sea anemone from the vicinity of hydrothermal vents in the Mariana back-arc basin, western North Pacific. Belonging to family Actinostolidae, *Marianactis bythios* is one of the most conspicuous animals around low temperature vents, at a depth of about 3600 m. Its mesenteries are not arrayed according to the *Actinostola* rule, it lacks basal tentacular thickenings, it has six pairs of complete mesenteries, and all its stronger mesenteries (members of the first three cycles) are gametogenic. It is further distinguished by having microbasic amastigophores in its tentacles. The final portion of Carlgren's (1949) key to the Actinostolidae is revised to accommodate *Marianactis* and other recent taxonomic changes in the family.

In April and May 1987, scientists discovered deep-sea hydrothermal vents and an associated faunal community in the Mariana back-arc basin, NNW of Guam, at a depth of about 3600 m. Far from the previously studied East Pacific Rise, these vents are unconnected to it by any intermediate spreading center.

Not surprisingly, much of the Mariana vent fauna is new (Hessler et al. 1988), including the relatively large sea anemone we describe here. One of the most conspicuous animals around low temperature vents, this member of family Actinostolidae belongs to a new genus and species, *Marianactis bythios* (Fig. 1). Actinians found on the Galapagos Spreading Center (Hessler & Smithey 1983) were too poorly preserved for detailed taxonomic study. The first species of actinian described from deep sea vents, *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, was collected on the French *Biocytherm 1* expedition around vents at 11°N in the Pacific, at 2000 m depth.

We detected no specializations to this unusual habitat in *M. bythios*, an anatomically unremarkable member of a predominantly

deep water family. This ordinariness contrasts with many new species of other groups from vent habitats. *Marianactis* is distinguished by a suite of characters that individually occur in other of the approximately 20 genera comprising the Actinostolidae, as well as by microbasic amastigophores in its tentacles.

Materials and Methods

Field work relied on the submarine *Alvin*. Photographs were taken with a hand-held camera through the view ports, and with a Photosea M2000 stereocamera held by one of the mechanical arms. Video recordings were made with an Osprey video camera mounted on the same arm.

Eight specimens were collected using *Alvin*'s mechanical arm. Placed in an insulated container for transport to the surface, they were not exposed to temperatures higher than 10°C. Once on the surface, seven specimens were preserved in either 10% formalin or alcohol; one was initially frozen, and later formalin-preserved.

Paraffin sections 8 μ m thick were stained with hematoxylin and eosin. Cnidae mea-

surements were on undischarged capsules in squash preparations. In the section "Distribution and size of cnidae," "n" refers to the number of capsules measured, and "N" is the proportion of animals examined in which that type of cnida was present. A measurement in parentheses was from a single capsule falling considerably outside the range of the others. Not all tissues of each specimen were studied. Microscopy, including photomicrography, was with a Reichert Ultrastar equipped with Nomarski interference contrast optics, and an automatic exposure camera.

Marianactis, new genus

Definition. — Actinostolidae with well developed pedal disc. Column smooth; diameter about equal to height; mesoglea firm. Sphincter moderately strong; tentacles can be completely covered in retraction. Tentacles of uniform thickness entire length; outer much shorter than inner; arrayed in several cycles on marginal half of oral disc. Longitudinal tentacle and oral disc circular musculature ectodermal; that of tentacles equally well developed on all sides. Microbasic amastigophores in tentacles. Fewer tentacles than mesenteries. Mesenteries not arrayed according to *Actinostola* rule; six pairs complete; all stronger ones fertile; two symmetrically arrayed siphonoglyphs attach to directive mesenteries; retractor muscles diffuse, parietobasilar muscles present. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores, microbasic amastigophores.

Type species. — *Marianactis bythios*, new species.

Etymology and gender. — The name *Marianactis* is a composite of "Mariana," geographical locality of the first known occurrence of this taxon, and "actis," Greek literally for ray or beam, a term that is applied to many taxa of sea anemones. The gender of "actis," and hence of *Marianactis*, is feminine.

Differential diagnosis. — Most members of Actinostolidae inhabit deep water and are therefore known primarily from preserved specimens. The genus *Marianactis* resembles many other genera of this family in being colorless (in preservation), in having relatively thick mesoglea, and in possessing tentacles that are wrinkled in preservation. It has the following combination of diagnostic characters: 1) mesenteries not arrayed according to the *Actinostola* rule, 2) no basal tentacular thickenings, 3) six pairs of complete mesenteries, and 4) all the stronger mesenteries (that is, members of the first three cycles) gametogenic. *Marianactis* is distinguished from all other actinostolids by its tentacular microbasic amastigophores.

Marianactis most resembles *Anthosactis* Danielssen, 1890, which has microbasic *b*-mastigophores in its stinging batteries, and unequally developed longitudinal tentacle musculature. It is also quite similar to *Tealidium* Hertwig, 1882, which is papillose. The definition of genus *Isoparactis* greatly resembles that of *Marianactis*. Carlgren (1949) included it among the Actinostolidae, using the definition of Stephenson (1920), who created it for *Paractis ferax* Stuckey, 1909. Parry (1952) demonstrated that Stuckey's species is actually an acontiate anemone belonging to family Bathypheilliidae.

All taxa were diagnosed initially with Carlgren (1949) and subsequently from the original literature. In Carlgren's (1949:77–78) key to the Actinostolidae, *Marianactis* falls under option II ("mesenteries not arrayed according to the *Actinostola*-rule"), B ("all or all stronger mesenteries fertile"). Beyond that, the key requires revision not only to accommodate *Marianactis*. Carlgren's descriptions of two additional genera of actinostolids were published posthumously—*Hadalanthus* Carlgren, 1956, and *Cnidanthea* Carlgren, 1959. In addition to *Isoparactis*, *Actinoscyphia* must be eliminated, because Riemann-Zürneck (1978) restored it

to its own family. Also, Carlgren (1949) used the letter "h" in two separate couplets/triplets. The last two-thirds of the key is revised to read as follows:

- B) All or all stronger mesenteries fertile (with the possible exception of directives)
- f) Longitudinal tentacle muscles mesogleal; at least 12 pairs of mesenteries complete
- g) Outer tentacles with basal battery of microbasic *b*-mastigophores on aboral side. Submarginal collar. Directives may be sterile
Hormosoma
- gg) Microbasic *b*-mastigophores of tentacles scattered, not arrayed in batteries. Directives fertile *Cnidanthus*
- ff) Longitudinal tentacle muscles ectodermal
- h) Microbasic *b*-mastigophores in tentacles; arrayed in batteries and may also be scattered
- i) Column with mesogleal papillae *Tealidium*
- ii) Column smooth; longitudinal tentacle muscles strongest on oral side *Anthosactis*
- hh) No microbasic *b*-mastigophores in tentacles
- j) Microbasic amastigophores in tentacles; six pairs of mesenteries complete *Marianactis*
- jj) Microbasic *p*-mastigophores in tentacles; six pairs of mesenteries complete; column divided into scapus and scapulus *Hadalanthus*
- jjj) No tentacular mastigophores
- k) At least 12 pairs of mesenteries perfect *Paranthus*
- kk) Six pairs of mesenteries perfect
- l) Sphincter very strong, forming a projecting wall. Mesenteries not hexamerously arrayed. Few, stout tentacles. May have distal papillae *Bathydactylus*
- ll) Sphincter strong but not forming a wall. Mesenteries hexamerously arrayed. Column with papillose nematocyst batteries *Cnidanthea*
- lll) Column smooth. More than 48 tentacles, closely packed at the rim, in at least 2 cycles *Epiparactis*
- BB) The oldest six pairs of mesenteries sterile, the other stronger mesenteries fertile
- m) Column divisible into scapus and capitulum. Possibly two sphincters
Pseudoparactis
- mm) Column not divisible into scapus and capitulum *Antiparactis*
- BBB) The oldest 12 pairs of mesenteries sterile *Pycnanthus*
- BBBB) The three oldest cycles of mesenteries sterile. Mesenteries not divided into filament-free fertile and filament-bearing sterile ones. Oral disc lobed. Sphincter very long *Antholoba*



Fig. 1. Bed of *Marianactis bythios* in situ. Probe diameter 1 cm.

Marianactis bythios, new species

Description.—Body form and size: Expanded preserved specimens columnar and colorless (white to yellowish); column diameter approximately equal to height. Contracted preserved specimens dome-shaped; height one-half to two-thirds diameter. Field notes, and measurements on photos and video recordings, indicate that expanded animals (Fig. 1) were up to “five inches [i.e., about 130 mm] across” the tentacle crown, but preserved ones 15–50 mm diameter. Column appears rugose in some specimens, probably due to contraction; ectoderm thin relative to body wall (Figs. 2, 4, 5); often entirely sloughed off.

Base: Flat; equal to column width or somewhat larger; 15–50 mm. Adherent in life.

Tentacles and oral disc: Tentacles color-

less in preservation, but photos and field observations note crowns pastel colored—mainly pinks and yellows. Tentacles arrayed in several cycles on peripheral half of oral disc; arise from indistinct margin where microbasic amastigophores may be densely packed (Fig. 6). Outer tentacles much shorter than inner; some outer tentacles merely stubs, inner to 15 mm length in animal 50 mm basal diameter. Tentacles taper slightly from base 1–2 mm in diameter to blunt point, but some swollen mid-way along length; transversely ridged in contraction; of equal thickness on all sides; lack basal thickenings. Fewer tentacles than mesenteries, but more than number of mesentery pairs; commonly about 60 tentacles. Oral disc capable of covering tentacles completely. Other details obscure due to contraction of most individuals examined.



Fig. 2. Cross section of *Marianactis bythios* at mid-column. Note regular array of mesenteries and diffuse retractor muscles. Fourth cycle mesenteries (X) are minimally developed, secondary mesenteries (S) are fertile, column mesoglea (M) is thick, and ectoderm (arrow) is thin. CAS 065172 (holotype).

Internal anatomy: Mesenteries regularly arrayed, not according to *Actinostola* rule (Fig. 2). Four cycles in most specimens; only first order complete and with small oral and marginal stomata; highest (fourth) order barely developed but seemingly wider proximally than distally, sterile, lacking filaments; filaments of penultimate (third) order absent from distal half. All except highest order (with possible exception of penultimate order in some individuals) fertile, including directives (Fig. 3). Only males seen; sexes presumably separate. Retractor muscles strong, diffuse, with increasingly wider processes centrally (Figs. 2, 3). Parietobasilar muscles with short detached pennon (Fig. 2); not evident at mid-body.

Sphincter muscle mesogleal, reticulate; composed of very small alveoli of uniform (Fig. 4) or slightly irregular (Fig. 5) size. Best



Fig. 3. Cross section through pair of fertile directive mesenteries, *Marianactis bythios*. CAS 065170.

developed at margin, tapering proximally; hugs endodermal side. Mesoglea on ectodermal side fibrous (Fig. 4).

Longitudinal musculature of tentacles strong, ectodermal; circular muscles not apparent. Oral disc circular muscles ectodermal, disrupted where tentacles insert on oral disc (Fig. 7).

Actinopharynx of typical actinostolid length and rugosity; white in color or rarely violet-brown (as is common in deep-water actinians); two symmetrical siphonoglyphs attach to directive mesenteries; siphonoglyphs not especially prolonged.

Cnidom: basitrichs, microbasic *p*-mastigophores, spirocysts, microbasic amastigophores.



Fig. 4. Longitudinal section of mesogleal sphincter of *Marianactis bythios*. CAS 065171.

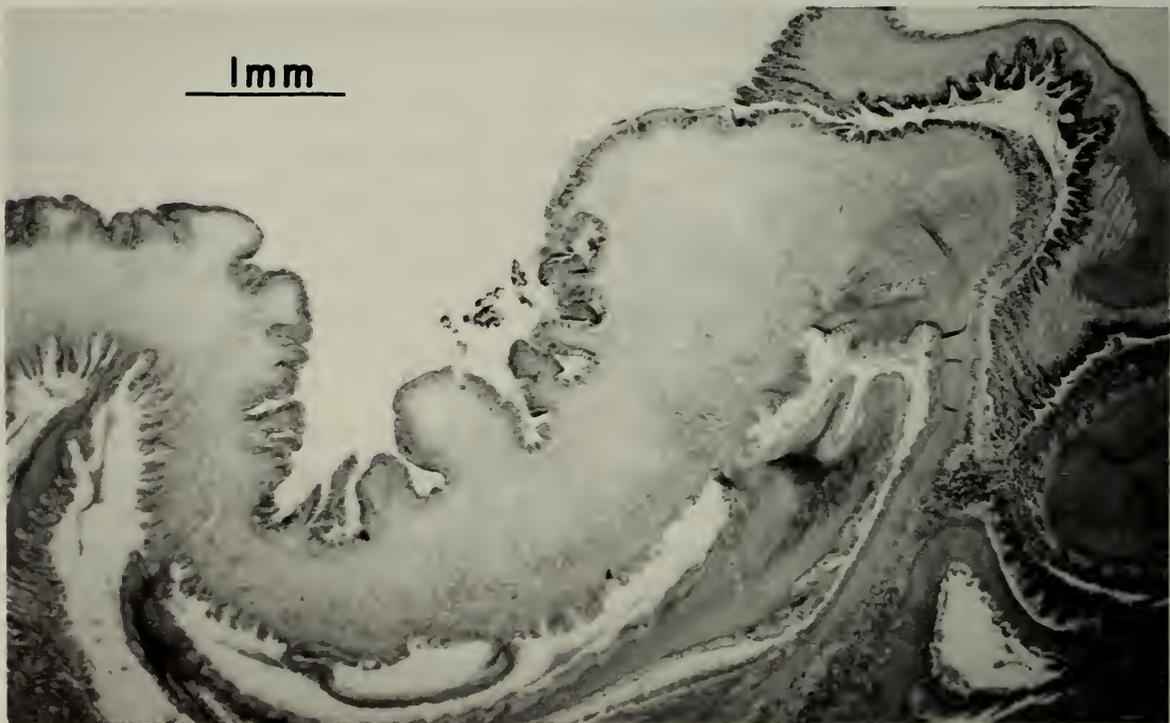


Fig. 5. Longitudinal section of mesogleal sphincter of *Marianactis bythios*. CAS 065172.



Fig. 6. Intersection of column and tentacles. Arrow indicates layer of microbasic amastigophores, *Marianactis bythios*. CAS 065172.

Distribution and size of cnidae.—(Letter corresponds to illustration in Fig. 8.)

Tentacles:

- spirocysts (A) (26.1) 27.5–49.2 (54.9)
× 2.5–4.7 μm n = 41 N = 4/4
- robust spirocysts (B) 43.6–73.1 ×
4.6–7.9 μm n = 35 N = 4/4
- basitrichs (C) 35.3–42.3 × 2.5–4.9
μm n = 34 N = 4/4
- microbasic amastigophores (D) 29.8–
36.0 × 4.3–5.0 (5.4) μm n = 18 N
= 2/3

Actinopharynx:

- microbasic *p*-mastigophores (E)
(27.3) 30.4–45.9 × 4.3–6.0 μm n
= 36 N = 3/3

Mesenterial filaments:

- microbasic *p*-mastigophores (F)
28.4–44.3 (48.0) × (3.9) 4.2–6.2
μm n = 44 N = 4/4

Column:

- basitrichs (G) (19.1) 20.3–27.3 (27.8)
× 2.3–3.7 μm n = 44 N = 4/4

Discussion.—Habitat, range, and natural history: The eight specimens of *Marianactis bythios* examined were collected from the Anemone Heaven portion of the Burke hydrothermal field (18°10.9'N, 144°43.2'E, 3660 m) and from the Alice Springs site (18°12.6'N, 144°42.4'E, average depth 3640 m). All were originally attached to rocks, although some were detached during collection.

Members of this species were the dominant inhabitants of the region peripheral to the vent openings. Population density was high in places, but tentacles of adjacent individuals generally did not make contact; the animals seemed to be evenly spaced. At both sites, the plume of vent water appeared quite “smoky.” Where emerging vent water was clear, such as at the Ilium field and the Snail Pits portion of the Burke field, this anemone occurred in smaller numbers. We can offer no explanation for this correlation.

Even individuals attached to rock near

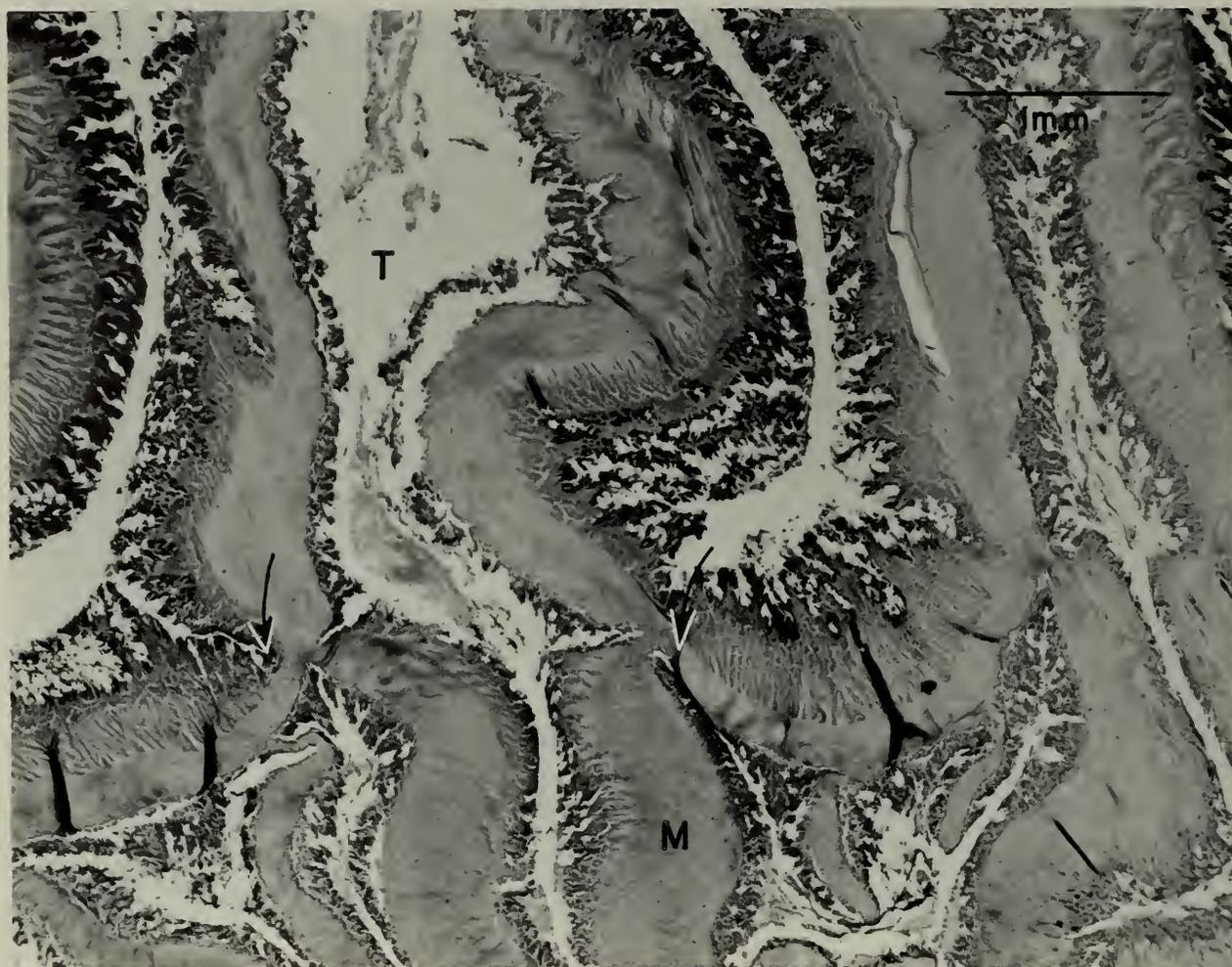


Fig. 7. Longitudinal section of *Marianactus bythios* at intersection of tentacles and oral disc. T = coelenteric space within tentacle; M = mesentery; arrows = region lacking ectodermal muscles. MNHN specimen.

the lip of the openings were never positioned where they were exposed to undiluted emerging vent water, unlike some crabs, snails, and shrimps, which occurred in the vent openings themselves. Therefore, it is unlikely that the actinians contacted water in excess of a degree or so over ambient, which is 1.6°C; more than a meter from the vent, water temperature was essentially ambient. At both sites, abundance of actinians declined with distance from the vent opening. They extended tens of meters from the emerging water, being found further from vent openings than organisms of any other taxa associated with the vents. The outermost edge of their distribution operationally defined the periphery of the vent field.

Many shallow water sea anemones possess intracellular algal symbionts that provide fixed carbon to their hosts (e.g., Muscatine 1974). Morphological and behavioral adaptations to them have evolved in some species (e.g., Lewis 1984). Several invertebrate taxa associated with hydrothermal vents bear endosymbiotic bacteria that oxidize reduced compounds (sulfide, methane), providing an energy source for their hosts (Childress et al. 1987; Stein et al. 1988). Therefore, we were especially alert for morphological evidence of symbionts in this anemone, but found none. Doumenc & VanPraët (1988) concluded that the diet of the vent actinian *Cyananthea hydrothermalis* includes bacteria, but that they are not in symbiosis.

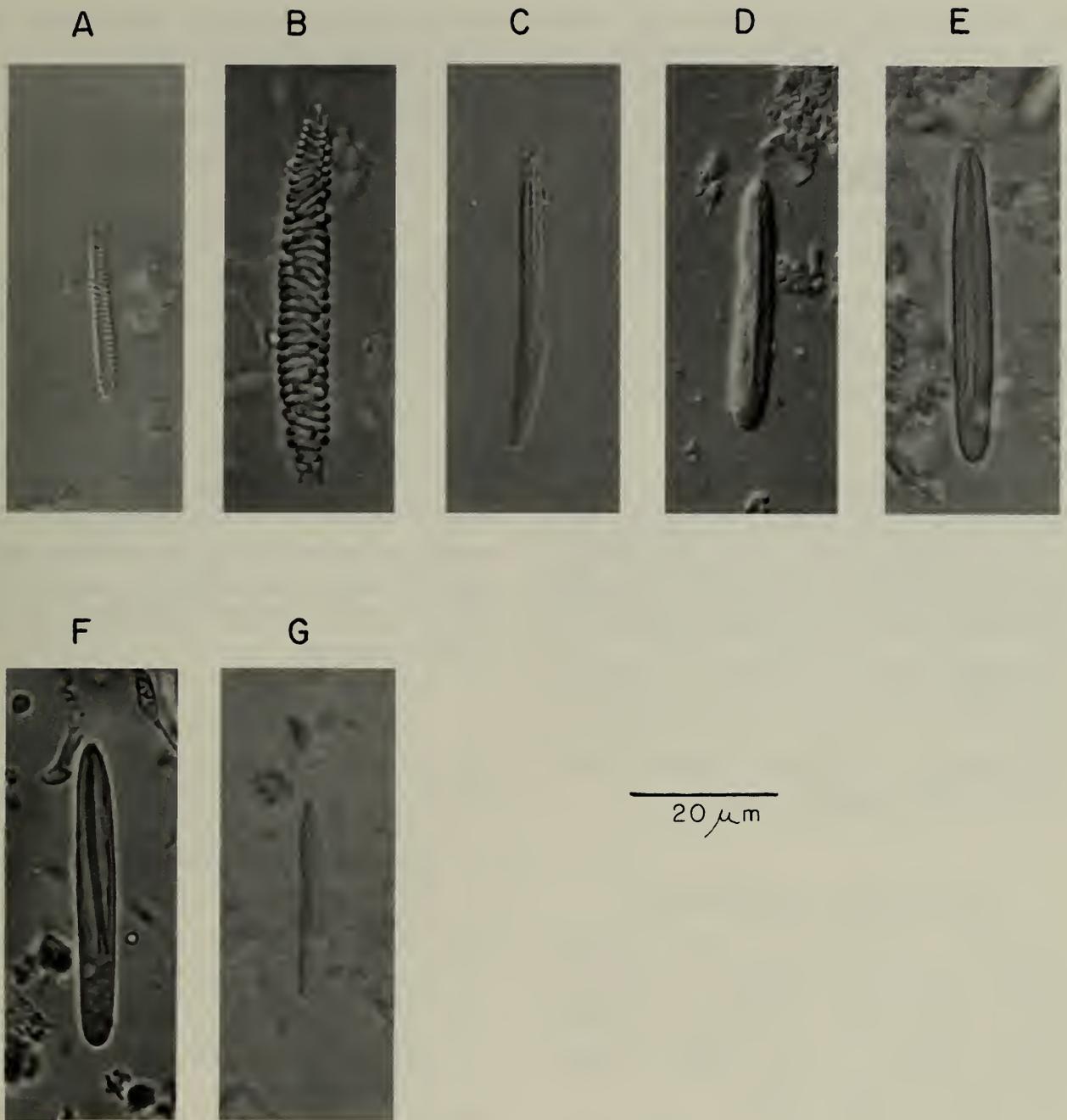


Fig. 8. Cnidae signature of *Marianactis bythios*. See text for explanation.

Nematocyst batteries: Whether the microbasic amastigophores of the tentacles are organized into batteries is uncertain. That type of cnida seems absent altogether from some individuals, and scattered in the tentacles of others. But the holotype has a dense layer of them (Fig. 6) in what is either the distalmost column or basalmost tentacles—with no distinct margin, a dividing line cannot be drawn. Carlgren's (1949) catalog refers repeatedly to nematocyst batteries, but contains no definition of the term. At least

for actinostolids, the implication is that the microbasic *b*-mastigophores in stinging batteries are extraordinarily large (e.g., Carlgren 1921, in the description of *Tealidium jungerseni*). The microbasic amastigophores of *M. bythios* are of unremarkable size.

Comparison with other vent species: The description of *Cyananthea hydrothermala* Doumenc & Van-Praët, 1988, the only previously described vent actinian, is incomplete and tentative, being based on a portion

of one poorly preserved specimen. Thus, some of its anatomy had to be inferred, and its attribution to family Actinostolidae was mainly due to the absence of acontia. Indeed, critical features such as mesenterial arrangement and whether nematocyst batteries are present seemingly could not be determined; hence our omission of it from our revised key. *Marianactis bythios* clearly differs from this species in cnidae (specifically tentacle basitrichs and spirocysts of our species are larger, and ours lacks columnar microbasic *p*-mastigophores), in tentacle arrangement, and in color.

Phylogenetic relationships within the Actinostolidae: Many genera of actinostolids, as is true in some other actinian families, are defined by unique combinations of characters rather than by singular features. It is this mosaic nature of diagnostic characters that makes inferences about evolution difficult.

Etymology: The specific epithet *bythios* means "of the deep" in Greek.

Type Locality and Specimens

Holotype.—Department of Invertebrate Zoology, California Academy of Sciences (CAS), catalog #065172; male; from Alice Springs, Mariana back-arc basin. Includes 10 microscope slides from it.

Paratypes.—CAS #065171; two specimens, one sectioned (male); from Anemone Heaven, Mariana back-arc basin. Includes 10 microscope slides from sectioned specimen.

CAS #065170; one specimen; male; from Alice Springs, Mariana back-arc basin. Includes 10 microscope slides from it.

National Museum of Natural History (USNM), catalog #84401; one specimen; from Burke field, Mariana back-arc basin; includes 10 microscope slides from it.

USNM #84402; one specimen; from Alice Springs, Mariana back-arc basin.

Museum Nationale d'Histoire Naturelle,

Paris (MNHN); one specimen; from Burke field, Mariana back-arc basin.

MNHN; one specimen; from Alice Springs, Mariana back-arc basin; includes 10 microscope slides from it.

Acknowledgments

Michel Boudrias and Scott France aided in collecting the material. Collection was supported by NSF grant OCE83-11258 and a grant from the National Geographic Society. Sections were cut and stained courtesy of Andromeda Systems. We thank Cadet Hand, Michael Kellogg, and Karen Riemann-Zümeck for critical and constructive reading of an earlier version of the manuscript, Verena Tunnicliffe for a copy of a relevant paper, and Jean de Mouthe for preparing the figures.

Literature Cited

- Carlgren, O. 1921. Actiniaria Part 1.—The Danish Ingolf-Expedition 5:1–241.
- . 1949. A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria.—Kungl. Svenska Vetenskapsakademiens Handlingar, Series 4, 1(1):1–121.
- . 1956. Actiniaria from depths exceeding 6000 meters.—Galathea Report 2:9–16.
- . 1959. Corallimorpharia and Actiniaria with description of a new genus and species from Peru.—Lunds Universitets Arsskrift, n.f. Avd. 2, 56(6):1–38.
- Childress, J. J., H. Felbeck, & G. N. Somero. 1987. Symbiosis in the deep sea.—Scientific American 255:115–120.
- Danielssen, D. C. 1890. Actinida.—Norwegian North-Atlantic Expedition 1876–1878, Zoology 19:1–184.
- Doumenc, D., & M. Van-Praët. 1988. Actinies abyssales d'un site hydrothermal du Pacifique oriental.—Oceanologica Acta special volume 8:61–68.
- Hertwig, R. 1882. Report on the Actiniaria dredged by H.M.S. *Challenger* during the years 1873–1876.—Scientific Results of the Voyage of H.M.S. *Challenger*, Zoology 6(1):1–136.
- Hessler, R. R., P. Lonsdale, & J. Hawkins. 1988. Patterns on the ocean floor.—New Scientist 1605:47–51.
- , & W. M. Smithey, Jr. 1983. The distribution

- and community structure of megafauna at the Galapagos Rift hydrothermal vents. Pp. 735–770 in P. A. Rona, K. Bostrom, L. Laubier, & K. L. Smith, Jr., eds., *Hydrothermal processes at seafloor spreading centers*. Plenum Press, New York and London.
- Lewis, J. B. 1984. Photosynthetic production by the coral reef anemone, *Lebrunia coralligens* Wilson, and behavioral correlates of two nutritional strategies.—*Biological Bulletin* 167(3):601–612.
- Muscatine, L. 1974. Endosymbiosis of cnidarians and algae. Pp. 359–395 in L. Muscatine & H. M. Lenhoff, eds., *Coelenterate biology: Reviews and new perspectives*. Academic Press, New York.
- Parry, G. 1952. The Actiniaria of New Zealand. A check-list of recorded and new species, a review of the literature and a key to the commoner forms. Part 2.—*Records of the Canterbury Museum* 6(2):121–141.
- Riemann-Zürneck, K. 1978. Tiefsee-Aktinien der Familie Actinoscyphiidae aus dem Nordatlantik (Actiniaria, Mesomyaria).—*Zoologica Scripta* 7:145–153.
- Stein, J. L., S. C. Cary, R. R. Hessler, S. Ohta, R. D. Vetter, J. J. Childress, & H. Felbeck. 1988. Chemoautotrophic symbiosis in a hydrothermal vent gastropod.—*Biological Bulletin* 174:373–378.
- Stephenson, T. A. 1920. On the classification of Actiniaria. Part I.—Forms with acontia and forms with a mesogloal sphincter.—*Quarterly Journal of Microscopical Science* 64 (new series): 425–574.
- Stuckey, F. G. A. 1909. A review of the New Zealand Actiniaria known to science, together with a description of twelve new species.—*Transactions of the New Zealand Institute* 41(for 1908):374–398.

(DGF) Department of Invertebrate Zoology, California Academy of Sciences, Golden Gate Park, San Francisco, California CA 94118; (RRH) Scripps Institution of Oceanography, La Jolla, California 92093.